Identifying open-pollinated populations of field corn as sources of cold tolerance for improving sweet corn

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Abstract

Sweet corn has poor cold tolerance and adaptation to the European Atlantic coast. Our objectives were to identify sources of favorable alleles for improving cold tolerance of three sweet corn hybrids, to compare sources of cold tolerance and early vigor, and to provide additional information on the relationships among different classes of loci and estimators of favorable alleles for cold tolerance. Each of ten field corn populations was crossed to four sweet corn inbreds. The field by sweet corn hybrids, the populations, the inbreds and the target hybrids were evaluated under cold conditions. Estimates of the mean frequencies of four classes of loci in the populations, and six estimators of favorable alleles ($lp_l\mu$', PTC, UBND, NI, PNG_g, and PNG_{ceg}) and GCA were computed. The population by inbred crosses were significantly different for emergence proportion and survival. Correlations between $lp_l\mu$', UBND, PTC and NI were high for emergence proportion. Most estimates of favorable alleles were significantly different from zero but not among populations. PTC was used to choose the best potential donor populations. The US Corn Belt Dent population AS-3(HT)C3 and the Spanish flint population Oroso were the best potential donors of favorable alleles for emergence proportion and survival under cold conditions, respectively. The ability to germinate and survive under cold conditions may be necessary, but it does not ensure adaptation to cold humid springs.

Key words: *Zea mays* L. - sweet corn - field corn populations - field by sweet corn hybrids - cold tolerance - favorable alleles.

Abbreviations: GCA, general combining ability; NI, net improvement; PNG_{ceg}, probability of net gain of favorable alleles given partial dominance or complementary epistasis; PNG_{g}, probability of net gain of favorable alleles given complete dominance; PTC, predicted three-way cross; UBND, minimum upper bound.

Introduction

Sweet corn does not grow well during the early stages of development in cold and humid environments such as the northwest of Spain (Ordás *et al*., 1994b). Sweet corn breeders are currently working on improving cold tolerance of sweet corn. Sweet corn is an endosperm mutant with physiological limitations and has a poorer germination, early vigor and growth rates than field corn (Hunsperger & Davis, 1987; Treat & Tracy, 1994).

Non-sweet corn germplasm has been successfully used to improve the agronomic performance of sweet corn (Tracy, 1994). The US Corn Belt Dent composite AS3(HT)C3 has been identified as a source of favorable alleles to improve yield of sweet corn for the European Atlantic conditions (Cartea *et al*., 1996a). The northwestern Spanish field corn population Tuy and the Spanish composite EPS6(S)C2 have been identified as sources of early vigor and adaptation of sweet corn to cold and humid springs (Cartea *et al*., 1996b). Early vigor and adaptation to cold humid springs require the ability to germinate under cold conditions. Such populations may therefore be potential donors of useful alleles for improving cold tolerance of sweet corn.

The identification of potential donors of cold tolerance can be done using classical methods, like general combining ability (GCA) (Sprague & Tatum, 1942) and predicted three-way cross (PTC) (Sprague & Eberhart, 1977), that are known to work well for any situation. PTC would be preferable to GCA if a sweet corn hybrid has particular performance deficiencies that can be solved with specific donors. Dudley (1984, 1987) developed a statistical procedure for estimation of the relative number of loci for which a donor population is different from each parent of the single cross designated to be improved ($lp_l\mu$'). Dudley's

theory of transfer of alleles goes further than GCA or PTC because it allows the election of the receiver parent of the hybrid.

Other methods have been developed as alternatives to Dudley's model: UBND (Gerloff & Smith, 1988a,b) is a minimum estimate of an upper bound on $lp_l\mu$, NI (Bernardo, 1990) estimates the relative number of favorable alleles that can be gained from the donor population minus the relative number of favorable alleles that can be lost from parents of the hybrid during selection, and PNG_g and PNG_{ceg} (Metz, 1994) estimate the relative number of loci where favorable alleles can be gained as a proportion of the relative number of loci where favorable alleles can be either gained or lost. PNG_g is used when complete dominance is present, and PNG_{ceg} when partial dominance or complementary epistasis are present.

Several authors have compared methods of identification of donors with favorable alleles (Gerloff & Smith, 1988a,b; Misevic, 1989a,b; Zanoni & Dudley, 1989; Bernardo, 1990; Cartea *et al*., 1996a,b, Malvar *et al*., 1997). These authors often report high correlations between most of the estimators, and present a different estimator as the most appropriate for each study. The calculation of several estimators of favorable alleles for a new situation may be convenient since there is no definitive evidence to choose any one estimator as the best.

For improving cold tolerance of sweet corn with field corn, most of the potential donors are expected to have higher cold tolerance than the receivers. This is common in plant breeding, when the objective is to improve a trait showing poorly in an otherwise elite hybrid, e.g., the improvement of sweet corn for agronomic performance, early vigor and diseases, pests and stress tolerance. Cartea *et al*. (1996a,b) and Malvar *et al*. (1997) looked for sources of agronomic performance and adaptation to the European Atlantic conditions of elite sweet

corn hybrids. Cartea *et al*. (1996a,b) found that $lp_l\mu$', PTC, UBND and NI identified the same populations as the best donors of agronomic performance and early vigor respectively. Malvar *et al*. (1997), working with field corn inbreds to improve sweet corn hybrids, also found high correlations between μG', PTC, UBND and NI. The statistics $lp_l\mu$' (Cartea *et al*., 1996a,b) and μG' (Malvar *et al*., 1997) along with other estimators of favorable alleles, can not be calculated sometimes due to failures in the assumptions of the model, particularly for traits other than yield. The reason for this failures in the assumptions may be that the theory of transfer of alleles was designed for improving elite hybrids for traits with complete dominance and no epistasis (Dudley, 1984, 1987), while in this study the hybrids are inferior to the potential donors for the traits of interest, dominance may be partial and epistasis may be present.

Our objectives were i) to identify sources of favorable alleles for improving cold tolerance of three sweet corn hybrids, ii) to compare sources of cold tolerance with sources of early vigor, and iii) to provide additional information on the relationships among different classes of loci and estimators of favorable alleles for cold tolerance traits.

Materials and methods

Ten field corn populations were evaluated as potential donors to improve three sweet corn hybrids (Table 1). In 1991 each population was crossed to each of the four sweet corn inbreds that were the parents of the three hybrids. The populations were used as males, and pollen from 160 plants in each population was collected to cross onto each sweet corn inbred. No more than 40 males were used each day to avoid collecting pollen from plants that had very similar flowering dates.

The ten populations *per se*, the 40 population x inbred crosses, the four sweet corn inbreds, and the three sweet corn hybrids to be improved were planted on trays filled with sterilized peat in a cold chamber. Two replications were planted in the cold chamber at a time. The planting was repeated three times to have six replications. Two plots were planted in each tray. Each two-row experimental plot consisted of 15 hills with one kernel per hill. Sowing depth was 2 cm. Rows were spaced 5 cm apart and hills 2 cm. Conditions were set as 14 hours with light at 14º C, and 10 hours without light at 8ºC. Light intensity was 2,000 Lux. The experiment was analyzed as a randomized complete block design with six replications.

The number of plants germinated was recorded every day, until germination ended, to calculate emergence score for each plot, using the formula:

$$\frac{(\Sigma(\text{number of plants emerged on a day / number of days after planting}))}{(\text{number of days from planting to the end of germination})}$$

Plant height was measured one month after planting, and measurements were repeated two weeks later to calculate plant growth. Plants were harvested one month after the end of germination. After harvest, shoots were dried to constant weight at 80ºC for five days, and dry

weight was recorded. Six traits were determined: proportion of emergence (%), emergence score (plants/day^2), dry shoot weight (mg/plant), survival (% of final plants over emerged plants), plant growth (increase on plant height, in mm, during two weeks), and plant vigor (just before harvest, using the scale 1 = poor, to 10 = excellent).

Analyses of variance and comparisons of means were performed for each trait. Means for each trait combined across replications were used to estimate the relative number of alleles for the classes of loci defined by Dudley (1987) for each sweet corn hybrid. The model developed by Dudley (1987) for two inbred parents of a hybrid, I_1 and I_2, and a potential donor population, P_y, considers four classes of loci. Loci at Class *i* are homozygous for the favorable allele in the single cross. Loci at classes *j* and *k* are heterozygous, with the favorable allele from parent 1 (class *j*) and from parent 2 (class *k*). Class *l* loci are homozygous for the less favorable allele in the single cross. Assumptions of this model include a constant genotypic value (μ) for all loci affecting the trait, complete dominance, and no epistasis. The donor is chosen based on the frequency of favorable alleles in class *l* ($lp_l\mu$'), calculated following Dudley (1987). Five other estimates of the value of each donor line were computed: predicted three-way cross (PTC) was computed as $((I_1 \times P_y) + (I_2 \times P_y)) / 2$ (Sprague & Eberhart, 1977); minimum upper bound on $lp_l\mu$ (UBND) was calculated as the minimum of the expressions $(I_1 \times P_y) - I_1$ and $(I_2 \times P_y) - I_2$ (Gerloff & Smith, 1988a,b); net improvement (NI) was the maximum of $(I_1 \times P_y) - (I_1 \times I_2)$ and $(I_2 \times P_y) - (I_1 \times I_2)$ (Bernardo, 1990); net gain of favorable alleles if complete dominance is prevalent (PNG_g) was the maximum of $lp_l\mu'/(jq_j\mu' + lp_l\mu')$ and $lp_l\mu'/(kq_k\mu' + lp_l\mu')$; and net gain of favorable alleles if partial dominance or complementary epistasis is prevalent (PNG_{ceg}) was computed as the maximum of $((I_1 \times P_y) -$

I_1) / (2(I_1 x P_y) - I_1 - P_y) and ((I_2 x P_y) - I_2 / (2(I_2 x P_y) - I_2 - P_y) (Metz, 1994). Finally, means for each trait across environments and sweet corn hybrids were used to compute general combining ability (GCA) effects (Sprague & Tatum, 1942).

The standard errors of estimators were calculated as the square root of the variance of the linear function associated with each estimator. Estimators were considered different from zero if they exceeded twice their standard error. Values for each estimator and within each sweet corn hybrid were considered significantly different when the difference among estimates exceeded twice the standard error of the difference.

For each trait and hybrid, simple correlation coefficients between each pair of estimators, and between each estimator and the performance *per se* of donor populations were calculated. Correlation coefficients for each of the seven sweet corn hybrids to be improved were then transformed by Fisher's z-transformation and tested for homogeneity. When homogeneity was found, a 90% confidence interval was calculated for the pooled correlation coefficient (Steel & Torrie, 1980). All the analyses were done with the SAS package (SAS, 1989).

Results and discussion

The sweet corn inbreds were significantly different for emergence proportion and score, plant growth, early vigor and survival (data not shown). The sweet corn hybrids were significantly different for emergence proportion, plant growth, shoot weight and survival. The field corn populations were significantly different for emergence proportion and score, plant growth and shoot weight. The crosses between the field corn populations and the sweet corn inbreds were significantly different for emergence proportion and survival.

The statistic $l\mathrm{p}_l\mu$' was highly correlated with PTC for emergence and survival proportions, and with UBND and NI for emergence proportion (Table 2). The correlations of $l\mathrm{p}_l\mu$' with UBND and NI varied for emergence because the relative importance of the classes of loci was not consistent among the three sweet corn hybrids. The expectation of UBND is $2l\mathrm{p}_l\mu$' + minimum ($2k\mathrm{p}_k\mu$', $2j\mathrm{p}_j\mu$'). For emergence proportion, the class $j\mathrm{p}_j\mu$' was abundant for the hybrids V679xEP58 and V679xEP60 and rare for I5125xEP60. The class $k\mathrm{p}_k\mu$' was rare for I5125xEP60 and V679xEP58 and common for V679xEP60 (Table 3). The correlation between $l\mathrm{p}_l\mu$' and UBND was 0.99 for V679xEP58, 0.77 for V679xEP60, and 0.95 for I5125xEP60; thus the pooled correlation was high but heterogeneous.

The expectation of PTC is $\mathrm{N}(z + \mu) + (i\mathrm{p}_i\mu' + i\mathrm{q}_i\mu' + j\mathrm{p}_j\mu' + k\mathrm{p}_k\mu' + l\mathrm{p}_l\mu' - l\mathrm{q}_l\mu')$. The statistic $i\mathrm{q}_i\mu$' was rare for the three hybrids, $l\mathrm{p}_l\mu$' was the most important class for the hybrid I5125xEP60 and one of the most important for V679xEP58, and for the hybrid V679xEP60, either $l\mathrm{p}_l\mu$' or $k\mathrm{p}_k\mu$' were high. Therefore, the pooled correlation was high between $l\mathrm{p}_l\mu$' and PTC. The expectation of NI is maximum ($l\mathrm{p}_l\mu' - k\mathrm{q}_k\mu'$), ($l\mathrm{p}_l\mu' - j\mathrm{q}_j\mu'$) (Bernardo, 1990). The pooled correlation between $l\mathrm{p}_l\mu$' and NI was high because $k\mathrm{q}_k\mu$' was negligible for two

hybrids, but it was heterogeneous because neither $k q_k \mu$' nor $j q_j \mu$' were negligible for the other hybrid.

The correlation between PNG_g, PNG_{ceg}, GCA, and actual value, and between these estimators and the previous estimators were not high (Table 2). Contrasting PNG_g with $l p_l \mu$', $l p_l \mu$' would tend to estimate the maximum potential of P_y to improve I_1 x I_2 without regard for the potential loss of favorable alleles in I_1 x I_2. PNG_g, in contrast, estimates the probability of net gain of favorable alleles from P_y without regard to the absolute magnitude of that potential gain. PNG_g has the expectation maximum $l p_l \mu$' / ($j q_j \mu$' + $l p_l \mu$'), $l p_l \mu$' / ($k q_k \mu$' + $l p_l \mu$'). If $j q_j \mu$' or $k q_k \mu$' were small PNG_g would tend to one, and no significant differences would be found among donors. In this experiment, PNG_g tended to one for two hybrids, and no significant differences were found among donors for any of the three hybrids.

Many authors have found high correlations between these estimators on field corn (Gerloff & Smith, 1988a,b; Misevic, 1989a,b; Zanoni & Dudley, 1989; Bernardo, 1990), and on sweet corn (Cartea *et al*., 1996a,b, Malvar *et al*., 1997). The correlations found in our experiment were not so high.

The abundance of $j p_j \mu$' reflects the importance of favorable alleles common to the sweet corn inbred V679 and several field corn populations. The inbred EP60 had some significant favorable alleles in common with some populations, while EP58 and I5125 had non significant frequencies of favorable alleles common to any of the field corn populations for emergence proportion. The most prevalent class of loci was *j* for emergence proportion for the hybrids V679xEP58 and V679xEP60, and the statistic $l p_l \mu$' for the hybrid I5125xEP60 (Table 3). The most rare statistic was $i q_i \mu$' for the hybrids V679xEP58 and V679xEP60, and

the class of loci *j* for the hybrid I5125xEP60. The class of loci *k* was not significantly different from zero for the hybrids V679xEP58 and I5125xEP60. Also, the estimators of classes of loci were not significant and positive for the hybrid I5125xEP60 except the statistic $lq_l\mu$'. Thus, the sweet corn inbred V679 has more favorable alleles for emergence under cold conditions than the inbreds EP58, EP60 and I5125. Caution is required if the inbred V679 is going to be improved using any of these populations because this inbred has favorable alleles for cold tolerance that can be lost during the selection program.

The field corn populations differed neither for their values of PNG_g, for emergence nor for survival proportion. Metz (1994) proposed using $lp_l\mu$' in conjunction with PNG_g. This would be interesting if PNG_g did not tend to one and significant differences were found among donors. The estimates of UBND and NI were not significantly different for emergence and survival proportions for the hybrids V679xEP58 and V679xEP60 and for survival proportions for the hybrid I5125xEP60. PTC was not significantly different among populations for survival proportion for the hybrid I5125xEP60. Finally, PNG_{ceg} was not significantly different for survival proportion for the hybrids V679xEP58 and V679xEP60. PTC would be appropriate if complete dominance was prevailing and PNG_{ceg} if partial dominance was more important. The statistics $lp_l\mu$' and PNG_g could not be calculated for several populations and, when they were calculated, the differences between populations were not significant. They were useful to know if a particular population has significant proportions of favorable alleles for improving a hybrid, but they did not allow the distinction between populations. Similarly, NI is useful to predict the probability of obtaining a net income from the breeding program, but it does not distinguish between populations. In contrast, the

populations were significantly different for their estimates of PTC because the expectation of PTC includes classes of loci that were important in this experiment.

For emergence proportion, all populations, except Tolosa, had significant and positive estimates of $lp_l\mu$' for the hybrid V679xEP58, though this statistic could not be calculated for EPS6(S)C2, and the differences between populations were not significant. The only populations with significant positive estimates of $lp_l\mu$' for the hybrid V679xEP60 were AS-3(HT)C3 and Tuy, though the differences between populations were not significant. The statistic $lp_l\mu$' could be calculated for half of the populations for the hybrid I5125xEP60, when it was calculated it was significant, and the differences between populations were not significant. Therefore, AS-3(HT)C3 and Tuy were the best potential sources of favorable alleles for increasing the emergence under cold conditions of the three sweet corn hybrids.

Most estimators of favorable alleles and PTC were positive and significantly different from zero for most populations for emergence and survival proportion, though there were many exceptions. Therefore, many of the field corn populations were identified as potential donors of favorable alleles for improving cold tolerance of sweet corn.

The populations with highest PTC for emergence proportion were AS-Z and Tuy for the hybrid V679xEP58, and AS-3(HT)C3 for V679xEP60 and I5125xEP60, and with highest PNG_{ceg} were EPS7(S)C2, Tolosa and Tremesino for the first hybrid, Ribadumia and EPS7(S)C2 for the second one, and EPS7(S)C2 for the last hybrid, though several populations did not significantly differ from the best ones for any hybrid. No parallelism was found between PTC and PNG_{ceg}.

The best potential donor for emergence proportion under cold conditions would be AS-3(HT)C3 if dominance is prevalent, and EPS7(S)C2 if partial dominance is more important. In our experiment, specific combining ability was significant for emergence proportion, therefore we may assume that dominance is important, thus AS-3(HT)C3 would be the best potential donor.

Most classes of loci could not be calculated for survival proportion for V679xEP60 due to failures of assumptions in the model (data not shown). The highest statistic for the other two hybrids was $l\mathrm{p}_l\mu$' and the lowest was $i\mathrm{q}_i\mu$', but the difference between the statistics was not as important for survival as it was for emergence. Most estimates of classes of loci, except $l\mathrm{p}_l\mu$' and several estimates of $j\mathrm{p}_j\mu$', were not significantly different from zero for survival proportion, thus, all field corn populations had significant proportions of favorable alleles for improving survival proportion of the sweet corn hybrids. The inbreds V679 and I5125 had significant proportions of favorable alleles common to the field corn populations for survival proportion, that were absent in the inbreds EP58 and EP60.

Almost all estimators of favorable alleles were significantly different from zero for survival proportion, except NI for V679xEP58. Therefore, all populations are potential sources of favorable alleles for improving survival proportion of the three sweet corn hybrids. However, no net improvement of V679xEP58 with any of these populations is expected.

The estimates of favorable alleles were not significantly different among populations except PTC for the hybrids V679xEP58 and V679xEP60, and $\mathrm{PNG}_{\mathrm{ceg}}$ for I5125xEP60 (Table 4), yet, most populations were not significantly different from the best potential donor.

Nevertheless, Oroso had the highest estimates of PTC for the first two hybrids and of PNG_{ceg} for I5125xEP60. Oroso had also the highest estimate of GCA for survival proportion.

The main risks for the evaluation of field corn populations as potential donors for improving the cold tolerance of sweet corn are that performance may change in a sweet corn background compared with a field corn background, and that table quality cannot be checked until the improved sweet corn hybrids are obtained. The predictions based on estimates of favorable alleles presumably save time and work. It is not worthwhile to convert every field corn variety to sweet corn before testing it as a possible source of favorable alleles.

Cartea *et al*., (1996b) identified Tuy and EPS6(S)C2 as potential sources of desirable alleles to improve early vigor and other agronomic traits in sweet corn hybrids. Cartea *et al*. (1996a) also found that Tuy, along with Oroso and AS-3(HT)C3, were the best populations for improving yield in sweet corn hybrids. In this experiment, Tuy and EPS6(S)C2 did not have high estimates of favorable alleles for improving cold tolerance, but Oroso and AS-3(HT)C3 were identified as the best potential donors of favorable alleles for improving cold tolerance. Consequently, the ability to germinate under cold conditions is necessary but it does not ensure the early vigor required for adaptation to cold humid springs. Furthermore, germplasm collected in cold areas, such as the population Viana, did not show cold tolerance under the conditions of this experiment. It seems that cold tolerance is a very complex trait and the place of origin of a population is not a sufficient warranty for possessing a high expression of the trait.

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Table 1. Name, pedigree and origin of sweet corn and field corn.

Name	Pedigree	Name	Origin
Sweet corn		**Field corn**	
Hybrids		Populations	
V679 x EP58		AS-3(HT)C3	Synthetic Univ.
V679 x EP60			of Minnesota[a]
I5125 x EP60		AS-Z	Synthetic Univ.
Inbred lines			of Minnesota[b]
EP58[e]	IL27a x I5125	EPS6(S)C2	Synthetic from humid
EP60[e]	IL27a x P51		Spain[c]
V679[g]	[(Me100xV1)O.P.xV643]	EPS7(S)C2	Synthetic from dry
	x Gold Cup		Spain[c]
I5125[h]	(IP39 x Tendermost) IP39	Oroso	Northwestern Spain[d]
		Ribadumia	Northwestern Spain[d]
		Tolosa	Northern Spain[d]
		Tremesino	Spanish race[f]
		Tuy	Northwestern Spain[d]
		Viana	Northwestern Spain[d]

[a] Peterson *et al*., 1976

[b] Ordás & Stucker, 1977

[c] Ordás, 1991

[d] Ordás *et al*., 1994a

[e] Ordás *et al*., 1994b

[f] Sánchez-Monge, 1962

[g] Kerr, 1968

[h] Gerdes *et al*., 1994

Table 2. Pooled correlations among $lp_l\mu$' , PTC, UBND, NI, PNG_g , PNG_{ceg} , GCA, and *per se* performance, and 90% confidence intervals (in parenthesis) for emergence proportion and survival proportion.

	Trait	PTC	UBND	NI	PNG_g	PNG_{ceg}	GCA	*Per se*
$lp_l\mu$'	Emergence	0.93 (0.70 0.98)	0.95*	0.95*	-0.27*	-0.63 (-0.90 0.01)	0.57 (-0.11 0.88)	0.04 (-0.61 0.66)
	Survival	0.94 (0.73 0.99)	0.77 (0.25 0.95)	0.75 (0.18 0.94)	0.15 (-0.56 0.73)	-0.46 (-0.86 0.27)	0.76 (0.21 0.94)	-0.27 (-0.74 0.55)
PTC	Emergence		0.78 (0.40 0.94)	0.81 (0.45 0.94)	0.10*	-0.45 (-0.81 0.15)	0.75 (0.32 0.92)	0.47 (-0.13 0.89)
	Survival		0.74 (0.31 0.92)	0.75 (0.32 0.92)	-0.12 (-0.72 0.58)	-0.56 (-0.85 0.00)	0.73 (0.28 0.91)	-0.05 (-0.60 0.52)
UBND	Emergence			0.85*	-0.55*	-0.24 (-0.71 0.37)	0.49 (-0.11 0.82)	0.29 (-0.33 0.73)
	Survival			0.00 (-0.32 0.74)	-0.38 (-0.83 0.36)	-0.55 (-.85 0.00)	0.06 (-0.01 0.22)	0.10 (-0.49 0.63)
NI	Emergence				0.30 (-0.42 0.79)	-0.53 (-0.84 0.05)	0.52 (-0.06 0.84)	0.12 (-0.48 0.64
	Survival				0.79 (0.28 0.95)	-0.21 (-0.69 0.40)	0.58 (0.00 0.86)	-0.08 (-0.01 0.51)
PNG_g	Emergence					0.15*	0.22 (-0.49 0.75)	0.10 (-0.57 0.69)
	Survival					0.70 (0.01 0.16)	0.18 (-0.54 0.74)	-0.18 (-0.75 0.53)
PNG_{ceg}	Emergence						-0.16 (-0.66 0.44)	0.33 (-0.28 0.75)
	Survival						-0.45 (-0.81 0.15)	0.73 (0.28 0.92)
GCA	Emergence							0.71 (0.30 0.90)
	Survival							0.01 (-0.60 0.60)

* Heterogeneous at the 5% level of probability.

[a] $l p_l \mu$' (Dudley, 1987), PTC (Sprague & Eberhart, 1977), UBND (Gerloff & Smith, 1988a,b), NI (Bernardo, 1990), PNG_g and PNG_{ceg} (Metz, 1994), and general combining ability (GCA) (Sprague & Tatum, 1942).

Table 3. Estimates [a] of relative number of alleles at six classes of loci, PTC, UBND, NI, PNG_g , PNG_{ceg}, GCA, and *per se* performance for ten field corn populations evaluated as sources of favorable alleles to improve emergence proportion of three sweet corn hybrids.

Estimators within each hybrid	Field corn populations									
	AS-3(HT)C3	AS-Z	EPS6(S)C2	EPS7(S)C2	Oroso	Ribadumia	Tolosa	Tremesino	Tuy	Viana
	V679xEP58									
$iq_i\mu$'	-4.72a	0.00a	[b]	-4.72a	-3.61a	-3.61a	-5.28a	-5.00a	-2.50a	-1.39a
$jp_j\mu$'	6.95*ab	8.33*ab	[b]	11.95*a	4.72ab	10.83*a	7.30*ab	4.17ab	11.39*a	0.83b
$jq_j\mu$'	6.66*ab	5.28ab	[b]	1.66b	8.89*ab	2.78b	6.31ab	9.44*ab	2.22b	12.78*a
$kp_k\mu$'	-0.56a	-0.56a	[b]	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a
$kq_k\mu$'	-0.56a	-0.56a	[b]	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a	-0.56a
$lp_l\mu$'	9.17*a	11.94*a	[b]	6.67*a	8.06*a	9.17*a	4.64a	10.56*a	9.17*a	9.44*a
PTC	80.56*abc	87.50*a	81.39*abc	80.56*abc	76.11*bcd	84.44*ab	71.86*d	80.56*abc	85.00*a	75.00*cd
UBND	17.22*a	22.77*a	10.00a	12.22*a	15.00*a	17.22*a	8.17a	20.00*a	17.22*a	17.77*a
NI	9.72*a	12.50*a	6.95*a	7.22*a	8.61*a	9.72*a	5.20a	11.11*a	9.72*a	10.00*a

PNG_g	1.06*a	1.05*a	b	1.09*a	1.07*a	1.06*a	1.14a	1.06*a	1.06*a	1.06*a
PNG_{ceg}	1.49*ab	1.03*b	1.06ab	2.00*a	1.48*ab	1.26*ab	1.95*a	1.61*a	1.17*ab	1.23*ab
					V679xEP60					
$iq_i\mu'$	-0.63ab	-4.03bc	-2.36abc	-9.45*c	-1.39ab	-7.92*bc	-1.57abc	-4.59bc	-4.03bc	3.89a
$jp_j\mu'$	8.27*a	1.53b	8.76*a	4.45*ab	4.17ab	3.75ab	8.24*a	1.81b	7.09*ab	3.34ab
$jq_j\mu'$	2.57b	9.31*a	2.09b	6.39*ab	6.67*ab	7.09*ab	2.60b	9.03*a	3.75ab	7.50*ab
$kp_k\mu'$	2.57a	7.64*a	2.09a	4.72a	5.00*a	5.42*a	2.60a	7.36*a	3.75a	5.83*a
$kq_k\mu'$	6.60*a	1.53a	7.09*a	4.45*a	4.17a	3.75a	6.57*a	1.81a	5.42*a	3.34a
$lp_l\mu'$	6.04*a	3.75a	2.91a	1.39a	2.50a	3.19a	1.48a	2.64a	4.86*a	3.05a
PTC	91.81*a	85.56*abc	85.56*abc	80.83*c	83.06*bc	84.44*abc	82.70*bc	83.33*bc	89.44*ab	84.17*abc
UBND	17.22*a	10.56a	10.00a	11.67*a	13.34*a	13.89*a	8.17a	8.89a	17.22*a	12.78*a
NI	3.47a	2.22a	0.83a	-3.06a	-1.67a	-0.56a	-1.12a	0.83a	1.11a	-0.28a
PNG_g	0.70*a	0.71a	0.58a	0.24a	0.37a	0.46a	0.36a	0.59a	0.56*	a0.48a
PNG_{ceg}	0.82*bc	1.90*b	1.06bc	6.99*a	0.71*bc	2.50*a	0.80bc	2.67ab	1.03*bc	bc0.47*c
					I5125xEP60					
$iq_i\mu'$	b	-1.11b	-2.92b	-3.61b	b	-11.67*a	b	-1.11b	b	b

$jp_j\mu$'	[b]	-2.50a	0.00a	-1.67a	[b]	-0.14a	[b]	-3.33a	[b]	[b]
$jq_j\mu$'	[b]	-1.95a	-4.44*a	-2.78a	[b]	-4.31*a	[b]	-1.11a	[b]	[b]
$kp_k\mu$'	[b]	-1.39a	-2.78a	-1.39a	[b]	-2.64a	[b]	-1.11a	[b]	[b]
$kq_k\mu$'	[b]	-1.39a	0.00a	-1.39a	[b]	-0.14a	[b]	-1.67a	[b]	[b]
$lp_l\mu$'	[b]	7.78*a	11.67*a	7.50*a	[b]	7.08*a	[b]	7.78*a	[b]	[b]
PTC	89.86*a	77.22*cd	86.11*ab	77.50*bcd	73.06*d	76.94*cd	81.67*abc	76.67*cd	81.67*abc	72.50*d
UBND	20.00*a	10.56ab	17.78*a	11.67*ab	1.67b	8.89ab	12.78*ab	8.89ab	8.33ab	1.11b
NI	18.75*a	9.72*ab	16.11*ab	10.28*ab	11.11*ab	11.39*ab	14.17*ab	9.45*b	16.39*ab	10.84*ab
PNG_g	[b]	1.33*a	1.62*a	1.59*a	[b]	2.55*a	[b]	1.27*a	[b]	[b]
PNG_{ceg}	1.00*b	1.92*ab	0.97*b	6.99*a	0.71*b	2.50*ab	1.00*b	2.67ab	0.90*b	2.00*ab
GCA	5.54*a	2.69abcd	4.08abc	-0.64bcde	5.09*ab	1.02abcd	-2.90de	-1.06cde	3.66abc	-5.92*e
Per se	83.9abc	82.8abc	81.1abc	88.9ab	75.0cd	89.4a	76.7cd	81.7abc	88.3ab	65.6d

* Exceeded twice the standard error. Means with the same letter within the same row do not differ significantly (LSD 0.05)

[a] The classes of loci $i q_i \mu$' to $l p_l \mu$' (Dudley, 1987), PTC (Sprague & Eberhart, 1977), UBND (Gerloff & Smith, 1988a,b), NI (Bernardo, 1990), PNG_g and PNG_{ceg} (Metz, 1994), and general combining ability (GCA) (Sprague & Tatum, 1942).

[b] The estimator cannot be calculated (Dudley, 1987 and Metz, 1994).

Table 4. Estimates [a] of $lp_l\mu$', PTC, UBND, NI, PNG_g , PNG_{ceg}, GCA, and *per se* performance for ten field corn populations evaluated as sources of favorable alleles to improve survival proportion of three sweet corn hybrids.

Estimators within each hybrid	Field corn populations									
	AS-3(HT)C3	AS-Z	EPS6(S)C2	EPS7(S)C2	Oroso	Ribadumia	Tolosa	Tremesino	Tuy	Viana
					V679xEP58					
$lp_l\mu$'	0.08*a	0.07*a	0.11*a	0.08*a	0.12*a	0.10*a	0.09*a	0.10*a	0.10*a	0.10*a
PTC	0.85*ab	0.84*ab	0.89*ab	0.85*ab	0.93*a	0.88*ab	0.83*b	0.87*ab	0.90*ab	0.90*ab
UBND	0.22*a	0.17*a	0.29*a	0.20*a	0.29*a	0.26*a	0.18*a	0.26*a	0.26*a	0.25*a
NI	0.04a	0.05a	0.08a	0.05a	0.09a	0.06a	0.08a	0.06a	0.07a	0.08a
PNG_g	0.69*a	0.81*a	0.76*a	0.77*a	0.81*a	0.73*a	0.94*a	0.74*a	0.78*a	0.83*a
PNG_{ceg}	1.29*a	1.34*a	1.01*a	0.90*a	1.16*a	1.50*a	1.76*a	0.99*a	0.85*a	0.80*a
					V679xEP60					
$lp_l\mu$'	[b]	[b]	[b]	[b]	[b]	0.14*a	0.16*a	0.14*a	[b]	[b]
PTC	0.88*ab	0.83*b	0.91*ab	0.87*ab	0.93*a	0.86*ab	0.91*ab	0.86*ab	0.90*ab	0.89*ab

UBND	0.22*a	0.17*a	0.29*a	0.20*a	0.29*a	0.26*a	0.30*a	0.26*a	0.26*a	0.25*a
NI	0.15*a	0.13*a	0.15*a	0.16*a	0.16*a	0.14*a	0.16*a	0.14*a	0.15*a	0.14*a
PNG_g	b	b	b	b	b	1.03*a	1.02*a	1.03*a	b	b
PNG_{ceg}	1.29*a	1.34*a	0.94*a	0.90*a	1.16*a	1.46*a	0.92*a	1.03*a	0.92*a	0.90*a
					I5125xEP60					
$lp_l\mu$'	0.27*a	0.27*a	0.29*a	0.29*a	0.28*a	0.27*a	0.28*a	0.28*a	0.28*a	0.28*a
PTC	0.81*a	0.81*a	0.84*a	0.86*a	0.83*a	0.80*a	0.84*a	0.86*a	0.84*a	0.83*a
UBND	0.59*a	0.64*a	0.66*a	0.68*a	0.62*a	0.67*a	0.68*a	0.68*a	0.65*a	0.66*a
NI	0.24*a	0.22*a	0.24*a	0.25*a	0.26*a	0.20*a	0.23*a	0.23*a	0.24*a	0.24*a
PNG_g	0.90*a	0.84*a	0.86*a	0.87*a	0.91*a	0.80*a	0.84*a	0.84*a	0.87*a	0.85*a
PNG_{ceg}	1.48*ab	1.17*ab	1.15*ab	1.01*b	1.57*a	1.41*ab	1.05*b	1.03*b	1.13*ab	1.06*b
GCA	-0.03*e	-0.03*e	0.01*b	0.00c	0.03*a	-0.01*d	-0.02*d	0.01*b	0.02*b	0.02*b
Per se	0.90ab	0.84ab	0.86ab	0.80b	0.95ab	0.97a	0.82ab	0.85ab	0.84ab	0.81ab

* Exceeded twice the standard error. Means with the same letter within the same row do not differ significantly (LSD 0.05)

[a] $l p_l \mu'$ (Dudley, 1987), PTC (Sprague & Eberhart, 1977), UBND (Gerloff & Smith, 1988a,b), NI (Bernardo, 1990), PNG_g and PNG_{ceg} (Metz, 1994), and general combining ability (GCA) (Sprague & Tatum, 1942).

[b]The estimator cannot be calculated (Dudley, 1987 and Metz, 1994).